Paul BERTHET

Laboratoire de Zoologie Systématique,
Université de Louvain,
Louvain, Belgium

3.3.6 The metabolic activity of oribatid mites (*Acarina*) in different forest floors

1. INTRODUCTION

After the pioneer work of B o r n e b u s c h in 1930, it took nearly twenty years before a systematic study of the respiratory activity of the soil fauna was attempted. In his remarkable papers on Nematodes and Enchytraeids, N i e l s e n (1949, 1961) considered the "possibility of estimating the share of the entire population in soil metabolism and ultimately, of their quantitative importance in the household of Nature" (N i e l s e n 1961). Afterwards, different authors applied this approach to other terrestrial populations or communities (S m a l l e y 1960, E n g e l m a n n 1961, P h i l l i p s o n 1962, B e r t h e t 1963, 1964, P h i l l i p s o n and W a t s o n 1965).

In 1948, M a c f a d y e n had already proposed the term of energy flow to describe in a general and quantitative manner the metabolic activity of the fauna in its biotope. For soil organisms, the energy flow may be estimated from the oxygen consumed by the animals, since it may be assumed that only a small part of the assimilated energy is used to perform biosynthesis.

In the present study, the oxygen-consumption measured in the laboratory was taken as an estimate of the respiratory activity of animals in natural conditions. These data, combined with measured population densities, were used to compute the energy flow rate through Oribatid communities in different biotopes. We feel that these results not only provide an estimate of the activity of Oribatid mites in the forest floor, but also provide an insight into the structure of the communities from a metabolic point of view.

2. MATERIALS AND METHODS

2.1 SITES AND SAMPLING

Eleven different communities were investigated; two of which were studied twice at a three year interval. The sites are described in Table I; they are all located within a 4 km radius in Moyenne-Belgique (4° long E, 50° lat N).

The fauna analysis performed by L e b r u n (1965), C o r b i s i e r (1965), H e b r a n t (1962) and E l s e n (1965) were used as primary data for the present paper. Generally, the aim of these investigators was to compare animal communities or distribution patterns of different species of *Oribatei*. Although their sampling method is not perfectly adapted for the present purpose, their results provide a fairly satisfactory basic material for the present study. Litter samples (the unaltered dead remains of plants down to the *Fx* layer) of 40 cm³ were collected in the different sites. Since constant volume samples were taken, they correspond to variable areas, according to sites and seasons (between 15 cm² in winter and 35 cm² in summer).

The faunal community I comes from an oakwood studied in 1961 by L e b r u n (1965) by monthly samples of 25 units; the metabolic activity of this fauna was the subject of a paper published elsewhere (B e r t h e t 1963, 1964). In 1964, C o r b i s i e r reinvestigated the same site (community II) and also the communities III, VII, X, XI, XII, XIII by collecting 15 samples every other month (C o r b i s i e r 1965). Communities IV, V and IX were studied the same year by Elsen who collected 25 samples every other month (E l s e n 1965).

Finally, we used to the data of Hebrant on the communities VI and VIII, based on one hundred samples collected every other month (H e b r a n t 1962, B e r t h e t and G é r a r d 1965, G é r a r d and B e r t h e t 1966).

2.2 THE FAUNA

The fauna was extracted by the usual Berlese-Tullgren funnels as described elsewhere (B e r t h e t 1954). Only adult *Oribatei* were counted since the systematic determination of larval and nymphal stages is not feasible in practice.

For all the communities considered, the fauna is represented by 87 species. Table II shows the sharing out of the species according to communities.

2.3 MEASUREMENT OF TEMPERATURE

The mean temperature of the litter over two week periods was recorded bimonthly by the Pallman's method modified by B e r t h e t (1960). This method is based on a polarimetric determination of the rate of inversion of a sucrose solution at a constant pH.

The temperature data were obtained in site I during 1961 and may be considered as representative of the temperature that was prevalent in sites VI and VIII investigated during the same year. During 1964, on the other hand, temperature was measured throughout the year in sites IV, V and IX; as the observed differences between these three sites were small, this average represents, in a quite satisfactorily manner, the temperatures for all the sites studied in 1964.

2.4 ESTIMATION OF THE INDIVIDUAL WEIGHT IN THE DIFFERENT SPECIES

The weight of the individuals of the different species is needed for computing the biomass as well as for estimating the metabolic activity. In a previous work (B e r t h e t 1963, 1964) the average mass of individuals belonging to about thirty species was determined by weighing; the weights of the animals belonging to other species were evaluated by comparison with animals of known weight.

In the present work, the mass of animals belonging to species not previously weighed was estimated from a multiple regression of log-weights against log-length and log-width; the two later data were obtained from the literature. The *Phthiracaroidea* were not taken into account in this computation since they differ too much in shape from other *Oribatei* species.

The regression equation obtained is:

$$W = L^{1.58} \cdot l^{1.45} \cdot 10^{-6.61}$$

where W is the weight in μg, L and l the length and the width in microns. The weights of *Phthiracaroidea* were estimated by comparison with values previously obtained from the species of this superfamily.

2.5 DETERMINATION OF THE O_2-CONSUMPTION OF A POPULATION

To estimate the oxygen consumption of Oribatid mites, we have used the previously established formula (B e r t h e t 1964), relating the oxygen consumption to the temperature and the weight of the animals. This relation was obtained in a study of the metabolic activity of individuals belonging to 16 species of *Oribatei*.

In the investigated range (between 0° and 15° C), the oxygen consumption was found to be considerably influenced by the temperature, the average Q_{10} being approximately equal to 4. Taking into account the variation of weights of the animals, the following equation obtained:

$$Y = 18.059 + 0.70 \ W - 0.487 \ Z$$

where: $Y = \log_{10}$ of the O_2 — consumption in 10^{-3} µl per individual, per day, $\ddot{W} = \log_{10}$ of weight in µg, $Z = 10^4/T$ where T is the absolute temperature.

To apply this equation to a population, the year was divided into as many periods as there are samplings, the date of the sampling determining the middle of each period. The average temperature in each period was calculated. The density of each species was assumed to remain constant during this period.

Under these conditions, for species s, during period p, one gets:

$$X_{sp} = 10\,(18.059 + 0.70\ W_s — 0.487\ Z_p) \cdot L_p \cdot D_{sp}$$

where: $X_{sp} = O_2$ — consummed in 10^{-3} µl per liter of litter by species s during period p, $W_s = \log_{10}$ of weight of species s in µg, $Z_p = 10^4/T$ at period p in days, $D_{sp} =$ number of individuals of species s per liter of litter during period p.

The calculation were performed with an I.B.M. 1620 computer.

3. RESULTS

3.1 TOTAL OXYGEN-CONSUMPTION

The average population density and biomass and the total O_2-consumption of each community, per liter of litter and per year, are given in Table III.

Communities I and II which were located at the same site and investigated respectively in 1961 and 1964, showed a high and identical metabolic activity and biomass. The *Oribatei* of community IV located in another oakwood, were also very numerous but, on the average, of smaller size than those of communities I and II. Their annual O_2-consumption was somewhat lower.

In coniferous forests (XII and XIII) and particularly in *Picea* (XIII), most Oribatid mites were of very small size (mainly *Eremeidae*) but at such a density that the metabolic activity of this fauna was still important.

In beech forests (communities X and XI) size of the individuals was not compensated by a high density and the O_2-consumption was low. Community III was located in an humid oakwood where litter decomposition was very rapid: large individuals were found (average weight 75 µg) but they were not numerous; their estimated oxygen-consumption amounted to only 33 ml per year.

3.2 SEASONAL INFLUENCES

Fig. 1 shows the change during the year of the amount of O_2-consumed per day, of biomass and density of adults *Oribatei*. This figure also gives the weight of the average individual of an ideal species which would account for all the oxygen consumed if its density was equal to the total density of this community. This average weight is:

$$W_A = \frac{Y_i - 18.059 + 0.487Z}{0.70}$$

where: $W_A = \log$ of the weight of this average individual in µg, $Y_i = \log$ of the mean oxygen consumption in 10^{-3} µl per individual per day, $Z = 10^4/T$.

It is observed that the peaks of metabolic activity occur during July, August and September, the warmest period of the year during which *Oribatei* reach their maximal density in litter. In autumn, however, the density of fauna remains high but the lowering of temperature decreases the oxygen consumption.

The results obtained at three year intervals (I and II, VI and VII), were similar although the population densities were higher in 1964 than in 1961.

Finally, it appears that metabolic activity of *Oribatei* in coniferous woods (XII and XIII) exhibits smaller seasonal variations than in the other communities: as soon as spring begins, a large increase of density leads to a great increase in metabolic activity, which only falls again during December and January.

3.3 CONTRIBUTION OF THE DIFFERENT SPECIES TO THE METABOLIC ACTIVITY

Fig. 2 shows the contribution of the various species to the total metabolic activity of Oribatid mites in the different sites. The area of each circle is proportional to the annual total of oxygen consumed, the area of each sector being proportional to the contribution of each species. Only those which accounted for more than 3% of the oxygen consumed, are represented separately. The total activity of the others is represented by the large white sector in which the number of such species is printed.

In general, less than 10 species, i.e. less than a fourth of the species present exhibit substantial activity. In all cases, four species account for at least 50% of the total metabolic activity of the community. From this point of view, the dominant species generally are those of large size, such as *Steganacarus magnus*, *Platynothrus peltifer*, or *Nothrus palustris*. In some communities however, species such as *Oribatula tibialis* or *Chamobates incisus* are sufficiently well represented to play a fairly important role. Finally, in coniferous woods, *Tectocepheus velatus* is present at such a high density that, in spite of its small size, it accounts for one quarter of the total amount of oxygen consumed.

4. DISCUSSION AND CONCLUSIONS

The sites where *Oribatei* activity is most intense are *Querceto-Carpinetum convallarietosum* (communities I and II) and *Querceto sessiliflorae* (IV); the first is a mull-moder, the second is a moder. In these communities, *Platynothrus peltifer* is particularly active. The two others *Querceto-Carpinetum convallarietosum* (III and V) also are mull-moder but established in humid locations. The litter is rapidly decomposed, mainly by the mesofauna; *Oribatei* are not numerous but they are represented by species of large size, such as *Nothrus palustris*, *Steganacarus magnus*, *Euzetes globulus*.

The other deciduous forests are moder-mor (VI and VII) or mor (IX, X, XI): the activity of *Oribatei* is weak, particularly in the two beach forests (X and XI) which are principally populated by species of small size.

Finally, the acid coniferous biotopes (XII and XIII) contain a very large number of individuals, forming a relatively small biomass; the amount of oxygen consumed is nevertheless very high. Once again, these results confirm from another point of view, the opposition between mull and mor.

On the other hand, the absolute value of oxygen consumption permits us to quantify the influence of Oribatid mites on the litter. In the favourable sites, the adults consume about one hundred ml of oxygen per year per liter of litter, which corresponds to 476 cal if it is assumed that the respiration quotient of edaphic animals is 0.82 (O'Connor 1962, Macfadyen 1963).

In a previous paper (Berthet 1964) we suggested that all the larvae and nymphs of *Oribatei* consume between one and two times the oxygen consumed by the adults. Thus, if the juvenile stages had been taken into account in the present work, the oxygen-consumption of all the *Oribatei* would be more than doubled and would amount to at least one thousand cal per liter per year.

It would have been better for our purpose, to have had data obtained by the analysis of samples of constant area rather than constant volume. The difference in thickness of the litter layer from one site to another would give a somewhat different picture if the energy flows were expressed on an area basis. However, for all sites and seasons, one may assume that, the litter has an average thickness of about 1.5 cm, corresponding to 15 liters of material per square meter. The flow of energy per square meter of litter is thus of the order of 15 Kcal per year.

It should be pointed out that the computations above deal only with the *Oribatei* of the litter. An estimate of the activity of these animals in forest soils, must include the contribution of the Oribatid mites inhabiting humus. From previous observations in community I (Berthet 1964), and preliminary results obtained on communities IV, V and IX, it appears that the activity of the *Oribatei* population is about the same in humus as in the litter. Thus, the oxygen consumed by all the *Oribatei* of forest soil, apparently corresponds to an energy flow of 30 Kcal per m².

This result is considerably higher than the value reported by Engelmann (1961) for the *Oribatei* fauna of an abandoned field; we have previously (Berthet 1964) pointed out the weaknesses of Engelmann's method for measuring the population densities and metabolic activities. On the other hand, our value is in agreement with Macfadyen's estimate concerning a grassland community (Macfadyen 1963).

On the basis of energy flow, *Oribatei* seem to play a much smaller role than some other edaphic animal groups: the activity of nematodes in grassland amounts to 150—350 Kcal per m² and per year (Nielsen 1949); for Enchytraeids in the sa memilieu, to 30—150 Kcal (Nielsen 1961). In a stand of Douglas fir, the activity of Enchytraeids was estimated to 150 Kcal (O'Connor 1962).

In fact, the energy consumption of *Oribatei* is very small when compared with the amount of food available. It is likely that in the various milieux investigated in the present study, the annual fall of dead leaves per square meter amounts to 300 g dry weight, i.e. more than 1.000 Kcal. It has been determined in various edaphic animals, such as Myriapods, Diplopods and Isopods (van der Drift 1950, Gere 1956, Dunger 1958a, 1958b, 1960, 1962, 1964, Bocock 1962) that the proportion of food assimilated during its passage through the digestive tract is usually less than 10% of that consumed. For *Oribatei*, the proportion assimilated also seems to be poor: 20% according to Engelmann (1961); 14% according to a previous study on *Steganacarus magnus* (Berthet 1964). If the latter figure is accepted, the flow of material through the digestive tract of *Oribatei* amounts to the equivalent of about 200 Kcal, although only 30 Kcal are completely metabolized. According to this estimate, *Oribatei* ingest about 20% of the organic material annually falling on the ground.

Numerous investigators have attempted to determine the diet of *Oribatei* (Riha 1951, Schuster 1956, Wallwork 1958, Hartenstein 1962a, b, c, d, e, f, g, Woodring and Cook 1962, Woodring 1963). It seems that one of the main items of the diet of *Oribatei* in mor could be mycelia; the animals would then, according to Macfadyen (1963), contribute to the process of humification by dispersing spores and preventing mycostasis or ageing of mycelial populations. In mull, on the other hand, the large *Oribatei* are mostly saprophagous and they could accelerate humification by fragmenting organic materials and favouring their microbial decomposition (van der Drift 1965). In this way, they could also have "a catalytic effect on the activity of microbes, which could be many times the magnitude of their own metabolic activity" (Macfadyen 1964).

REFERENCES

Berthet, P. 1954 — L'echantillonnage de la litière des forêts pour l'étude quantitative des populations d'acariens et de collemboles — Ann. Soc. R. Zool. Belg. 85: 5—22.

Berthet, P. 1960 — La mesure écologique de la température par détermination de la vitesse d'inversion du saccharose — Vegetatio, 9: 197—207.

Berthet, P. 1963 — Mesure de la consommation d'oxygène des Oribatides (Acariens) de la litière des Forêts (Soil organisms. Ed. J. Doeksen and J. van der Drift) — Amsterdam, 18—31.

Berthet, P. 1964 — L'activité des Oribatides (Acari: Oribatei) d'une chênaie — Mém. Inst. Roy. Sc. Nat. 152, 152 pp.

Berthet, P. and Gérard, G. 1965 — A statistical study of microdistribution of Oribatei (Acari). Part I. The distribution pattern. — Oïkos 16: 214—227.

Bocock, K. L. 1962 — The digestion and assimilation of food by Glomeris (Soil Organisms. Ed. J. Doeksen and J. van der Drift) — Amsterdam, 85—91.

Bornebusch, C. H. 1930 — The fauna of the forest soil — Forstl. Forskösv. Danm. 11: 1—256.

Corbisier, A. M. 1965 — Analyse d'affinité des synusies d'Oribates de la forêt de Meerdael — Mém. de licence, Louvain (unpublished), 86 pp.

Drift, J. van der, 1950 — Analysis of the animal community in a beech forest floor — Tijdschr. Ent. 94: 1—168.

Drift, J. van der, 1965 — The effect of animal activity in the litter layer (Experimental Pedology. Ed. Hallworth and D. V. Crawford) — London, 227—235.

Dunger, W. 1958a — Über die Zersetzung der Laubstreu durch die Boden-Mikrofauna im Auenwald — Zool. Jahrb. (Systematik), 86: 129—180.

Dunger, W. 1958b — Über die Veränderung des Fallaubes im Daum von Bodentieren — Zeitschr. f. Pflanzenernährung, Düngung u. Bodenkunde, 82 (127): 174—193.

Dunger, W. 1960 — Zu einigen Fragen der Leistung der Bodentiere bei der Umsetzung organischer Substanz — Zentralbl. f. Bakteriologie, Parasitenkunde, Infektionskrankheiten u. Hygiene, II, 113: 345—355.

Dunger, W. 1962 — Nahrungswahl bei Bodenarthropoden in produktionsbiologischer Sicht — 11 Internationaler Kongress für Entomologie. Wien 1960, 3: 169—173.

Dunger, W. 1964 — Tiere im Boden — Wittenberg-Lutherstadt, 265 pp.

Elsen, P. 1965 — Analyse de l'affinité spécifique entre les communautés d'Oribates de trois chênaies voisines — Mém. de licence, Louvain (unpublished), 136 pp.

Engelmann, M. D. 1961 — The role of soil Arthropods in the energetics of an old field community — Ecol. monogr. 31: 221—238.

Gérard, G. and Berthet, P. 1966 — A statistical study of microdistribution of Oribatei (Acari). Part II. The transformation of the date — Oïkos.

Gere, G. 1956 — The examination of the feeding biology and the humificative function of Diplopoda and Isopoda — Acta biol. acad. Sci. Hung. 6: 257—271.

Hartenstein, R. 1962a — Soil Oribatei. I. Feeding specificity among forest soil Oribatei (Acarina) — Ann. Ent. Soc. Amer. 55: 202—206.

Hartenstein, R. 1962b — Soil Oribatei. II. Belba kingi, new species (Acarina, Belbidae) and a study of its life history — Ann. ent. Soc. Amer. 55: 357—361.

Hartenstein, R. 1962c — Soil Oribatei. III. Studies on the development, biology and ecology of Metabelba montana (Kulez) (Acarina, Belbidae) and Eremobelba nervosa n. sp. (Acarina, Eremaeidae). — Ann. ent. Soc. Amer. 55: 361—367.

Hartenstein, R. 1962d — Soil Oribatei. IV. Observations on Ceratozetes gracilis (Acarina, Ceratozetidae) — Ann. ent. Soc. Amer. 55: 283—286.

Hartenstein, R. 1962e — Soil Oribatei. VI. Protoribates lophatrichus (Acarina, Haplozetidae) and its associations with micro-organisms — Ann. ent. Soc. Amer. 55: 587—591.

Hartenstein, R. 1962f — Soil Oribatei. V. Investigations on Platynothrus peltifer (Acarina, Camisiidae) — Ann. ent. Soc. Amer. 55: 709—713.

Hartenstein, R. 1962g — Soil Oribatei. VII. Decomposition on Conifer needles and deciduous leaf petioles by Steganacarus diaphanum (Acarina: Phthiracaridae) — Ann. ent. Soc. Amer. 55: 713—716.

Hebrant, F. 1962 — Recherche sur la mesure de l'agrégation — Mém. de licence, Louvain (unpublished), 142 pp.

Lébrun, Ph. 1965 — Contribution à l'étude écologique des Oribatides de la litière d'une forêt de Moyenne Belgique — Mém. de l'Inst. Roy. Sc. Nat. Belg. 153, 96 pp.

Macfadyen, A. 1948 — The meaning of productivity in biological systems — J. Anim. Ecol. 17: 75—80.

Macfadyen, A. 1963 — Animal Ecology, aims and methods — London, 344 pp.

Macfadyen, A. 1964 — Relations between mites and microorganisms and their significance in soil biology — Acarologia, h. s.: 148—149.

Nielsen, C. O. 1949 — Studies on the soil microfauna. II. The soil inhabiting nematodes — Nat. Jutland. 2: 1—131.

Nielsen, C. O. 1961 — Respiratory metabolism of some populations of Enchytraeid worms and freeliving Nematodes — Oïkos 12: 17—35.

O'Connor, F. B. 1962 — Oxygen consumption and population metabolism of some populations of Enchytraeidae form North Wales (Soil Organisms. Ed. J. Doeksen and J. van der Drift) — Amsterdam, 32—48.

Phillipson, J. 1962 — Respirometry and the study of energy turnover in natural systems with particular reference to harvestspiders (Phalangiida) — Oïkos, 13: 312—322.

Phillipson, J. and Watson, J. 1965 — Respiratory metabolism of the terrestrial isopod Oniscus asellus L. — Oïkos, 16: 78—87.

Riha, G. 1951 — Zur Ökologie der Oribatiden in Kalksteinböden — Zool. Jb. Syst., 80: 407—450.

Schuster, R. 1956 — Der Anteil der Oribatiden an den Zersetzungsvorgängen im Boden — Z. Morph. u. Oekol. Tiere, 45: 1—33.

Smalley, A. E. 1960 — Energy flow a salt marsh grasshopper population — Ecology, 41: 672—677.

Wallwork, J. A. 1958 — Notes on the feeding behaviour of some forest soil Acarina — Oïkos 9: 260—271.

Woodring, J. P. and Cook, E. F. 1962 — The biology of Ceratozetes cisalpinus, Scheloribates laevigatus and Oppia neerlandica (Oribatei) with a description of all stages — Acarologia 4: 101—137.

Woodring, J. P. 1963 — The nutrition and biology of Saprophytic Sarcoptiformes — Advances in Acarology 1: 89—111.

Table I

Main botanical features of the sites

Community No	Association	Date	Tree strata	Shrub strata	Herbaceous or muscinal strata
I	Querceto Carpinetum convallarietosum	1961	Quercus robur	Corylus avellana Carpinus betulus	Anemone nemorosa
II	idem	1964	idem	idem	idem
III	Querceto Carpinetum convallarietosum humid variant	1964	Quercus pedunculata	Corylus avellana Carpinus betulus	Lamium galeobdolon Anemone nemorosa
IV	Querceto sessiliflorae	1964	Quercus robur	Corylus avellana	Pteris aquilina Robus sp.
V	Querceto Carpinetum convallarietosum	1964	Quercus robur	Carpinus betulus	—
VI	Querceto sessiliflorae-Betuletum var. Leucobryum glaucum	1961	Quercus robur Quercus sessiliflora	Quercus robur Quercus sessiliflora	Leucobryum glaucum
VII	idem	1964	idem	idem	idem
VIII	Ruderalized site	1961	Populus canadensis	Prunus serotina Populus canadensis Larix europea	Urtica dioica
IX	Querceto sessiliflorae	1964	—	Quercus robur Betula verrucosa	—
X	Querceto Carpinetum convallarietosum (disturbed)	1964	Fagus silvatica	—	Pteris aquilina
XI	Querceto sessiliflorae-Betuletum (disturbed)	1964	Fagus silvatica	Fagus silvatica	Lonicera periclymenum Convallaria majalis
XII	Querceto roboris-Betuletum molinietosum (disturbed)	1964	Pinus silvestris	Quercus borealis	Vaccinium myrtillus
XIII	Querceto Carpinetum (disturbed)	1964	Picea abies	—	Hypnum cupressiforme

Table II
Distribution of oribatids in the different communities

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
Nanhermannia nanus (Nic.)	o	o	o	o	o	o	o	o	o	o	o	o	
Hypochthonius rufulus C. L. Koch	o	o	o	o	o	o	o	o	o	o	o		o
Eniochthonius minutissimus Berl.	o	o	o	o		o	o	o		o	o	o	o
Brachychthonius berlesei Willm.	o	o	o	o	o	o	o	o		o	o	o	o
Thrypochthoniellus excavatus (Willm.)				o	o				o				
Malaconothrus sp.		o											
Camisia spinifer (C. L. Koch)				o		o	o	o	o	o	o	o	o
Camisia segnis (Herm.)												o	o
Nothrus palustris C. L. Koch	o		o		o			o	o				
Nothrus silvestris Nic.	o	o	o	o	o	o	o	o	o	o	o	o	o
Platynothrus peltifer (C. L. Koch)	o	o	o	o	o	o	o	o	o	o	o	o	o
Hermannia gibba (C. L. Koch)	o		o										o
Micreremus brevipes (Mich.)	o		o		o	o		o	o				
Cymbaeremaeus cymba (Nic.)					o	o	o				o	o	
Amerus troisii (Berl.)	o										o	o	
Metabelba papillipes (Nic.)			o	o		o	o			o	o		
Dameus auritus C. L. Koch	o	o	o	o	o	o	o	o	o	o	o	o	o
Dameus onustus C. L. Koch	o			o									
Damaeobelba minutissima (Sell.)	o	o		o						o	o	o	o
Licneremaeus licnophorus (Mich.)			o	o	o		o					o	o
Fosseremus laciniatus (Berl.)					o			o					
Suctobelba subtrigona (Oudms.)	o	o	o	o	o	o	o	o	o	o	o	o	o
Suctobelba trigona (Mich.)	o	o	o	o	o	o	o	o	o	o	o	o	o
Oppia quadricarinata (Mich.)	o	o	o	o	o	o	o	o	o	o	o	o	o
Oppia nova (Oudms.)	o	o	o	o	o	o	o	o	o	o	o	o	o
Oppia ornata (Oudms.)	o	o	o	o	o	o	o	o	o	o	o	o	o
Oppia bicarinata (Paoli)						o		o					
Oppia fallax obsoleta (Paoli)		o	o	o	o		o			o	o		
Autogneta longilamellata (Mich.)							o						
Autogneta willmanni Dyrd.	o							o					
Oppia maritima (Willm.)		o		o									o
Oppia minus (Paoli)										o			
Oppia subpectinata (Oudms.)	o	o		o	o	o			o	o			o
Oppia translamellata (Willm.)			o	o	o		o	o					
Oppia splendens (C. L. Koch.)	o					o		o					
Oppia sp.			o										
Thyrisoma lanceolata (Mich.)						o	o	o				o	
Thyrisoma pectinata (Mich.)					o								
Ceratoppia bipilis (Herm.)			o	o	o	o	o	o	o			o	
Hermaniella granulata (Nic.)	o	o	o				o						
Tectocepheus velatus (Mich.)	o	o	o	o	o	o	o	o	o	o	o	o	o
Xenillus tegeocranus (Herm.)	o	o	o	o	o	o	o	o		o	o	o	
Odontocepheus elongatus (Mich.)	o			o		o	o						o
Cepheus cepheiformis (Nic.)	o	o	o	o	o	o	o	o	o		o	o	o
Cepheus latus C. L. Koch							o					o	
Cepheus dentatus (Mich.)		o					o						
Carabodes femoralis (Nic.)	o	o		o	o	o	o		o	o	o	o	o
Carabodes coriaceus C. L. Koch	o			o	o	o	o	o	o		o	o	o
Carabodes labyrinthicus (Mich.)	o		o	o		o		o		o	o	o	o
Carabodes marginatus (Mich.)	o	o	o	o			o			o	o	o	o
Adoristes ovatus (C. L. Koch)	o			o			o	o			o	o	o
Adoristes poppei (Oudms.)											o	o	o
Cultroribula juncta (Mich.)				o	o	o		o	o			o	
Liacarus coracinus (C. L. Koch)	o	o	o	o	o	o		o	o	o			o
Liebstadia similis (Mich.)		o	o	o		o	o		o		o	o	o
Oribatula tibialis (Nic.)	o	o	o	o	o	o	o	o	o	o	o	o	o
Zygoribatula exilis (Nic.)				o									
Gustavia microcephala (Nic.)				o									
Scheloribates confundatus Sell.				o					o				
Scheloribates latipes (C. L. Koch)				o									
Protoribates badensis Sell.							o						
Protoribates lagenula (Berl.)			o							o		o	
Edwardzetes edwardsii (Nic.)													o
Chamobates cuspidatus (Mich.)	o	)	o	o			o		o	o	o	o	o
Chamobates incisus v. d. Ham.	o	o	o			o	o	o	o	o	o	o	o
Ceratozetes mediocris Berl.							c					o	
Ceratozetes gracilis (Mich.)	o	o	o		o		o						
Euzetes globulus (Nic.)	o	o	o	o	o								
Melanozetes mollicomus (C. L. Koch)						o	o	o					
Diapterobates humeralis (Herm.)							o		o	o			o
Mycobates tridactylus Willm.													o
Punctoribates punctum (C. L. Koch)		o		o	o	o		o			o		
Minunthozetes semirufus (C. L. Koch)	o	o	o	o			o		o	o	o		o
Galumna lanceata Oudms.	o	o	o	o	o	o	o	o	o		o		
Galumna nervosa (Berl.)		o	o										
Tectoribates borussicus (Sell.)		o	o	o	o	o	o	o		o		o	o
Oribatella reticulata Berl.											o		
Oribatella quadricornuta (Mich.)	o	o	o	o	o	o	o	o	o	o	o	o	o
Parachipteria willmanni (v. d. Ham.)	o	o	o									o	o
Achipteria coleoptrata L.	o	o	o	o	o			o		o	o		o
Eupelops sp.	o	o				o		o		o	o		
Steganacarus striculus (C. L. Koch)		o	o							o			
Steganacarus magnus (Nic.)	o					o	o		o	o			
Phthiracarus piger (Scop.)		o	o	o	o	o	o	o	o	o	o	o	o
Phthiracarus ferrugineus (C. L. Koch)	o	o	o	o	o	o	o	o	o	o	o	o	o
Microtritia minima (Berl.)				o		o		o				o	o
Rhisotritia ardua (C. L. Koch)	o	o	o	o	o	o	o	o	o	o	o	o	o

Table III
Density, biomass and oxygen-consumption values of the oribatid fauna in the different communities

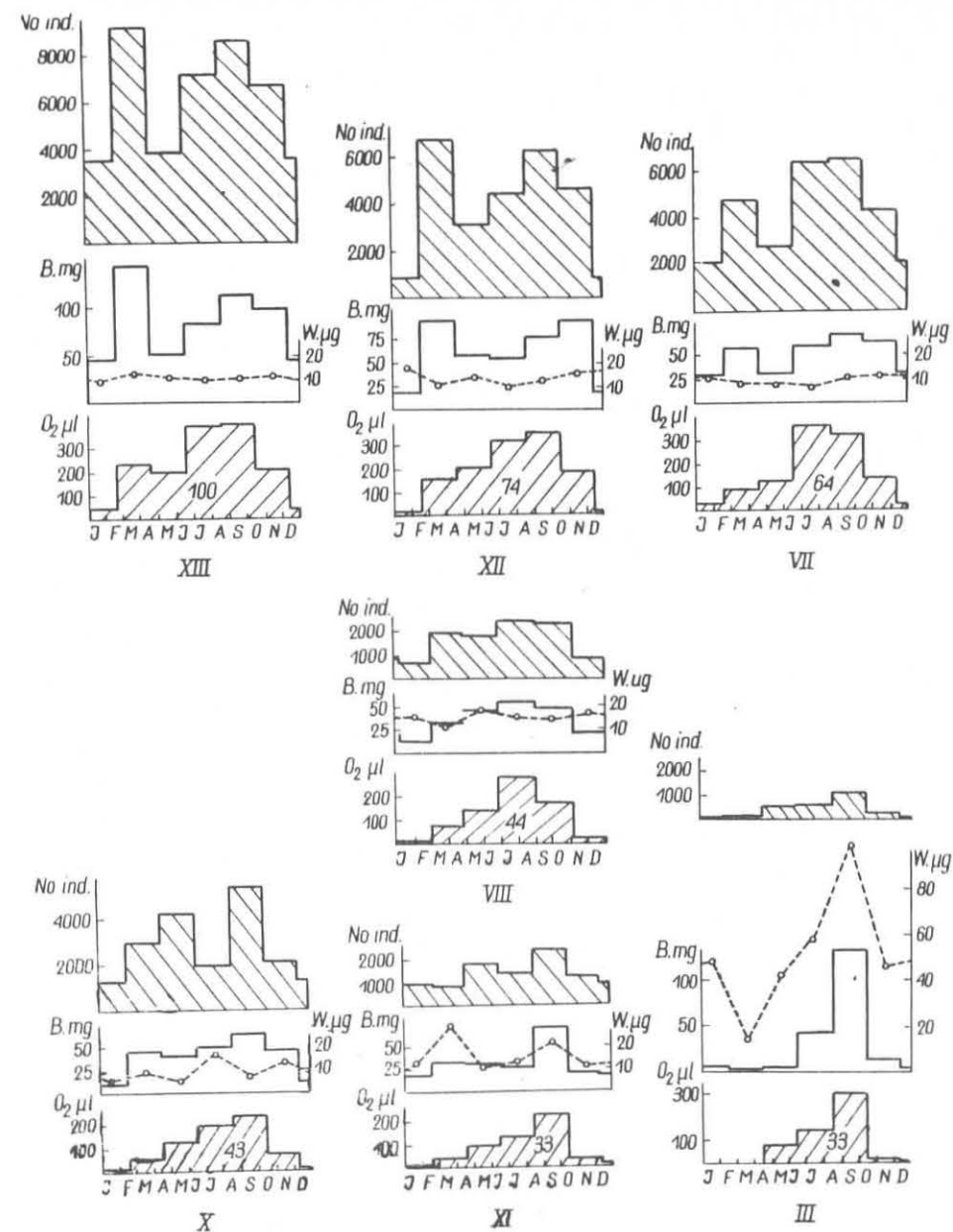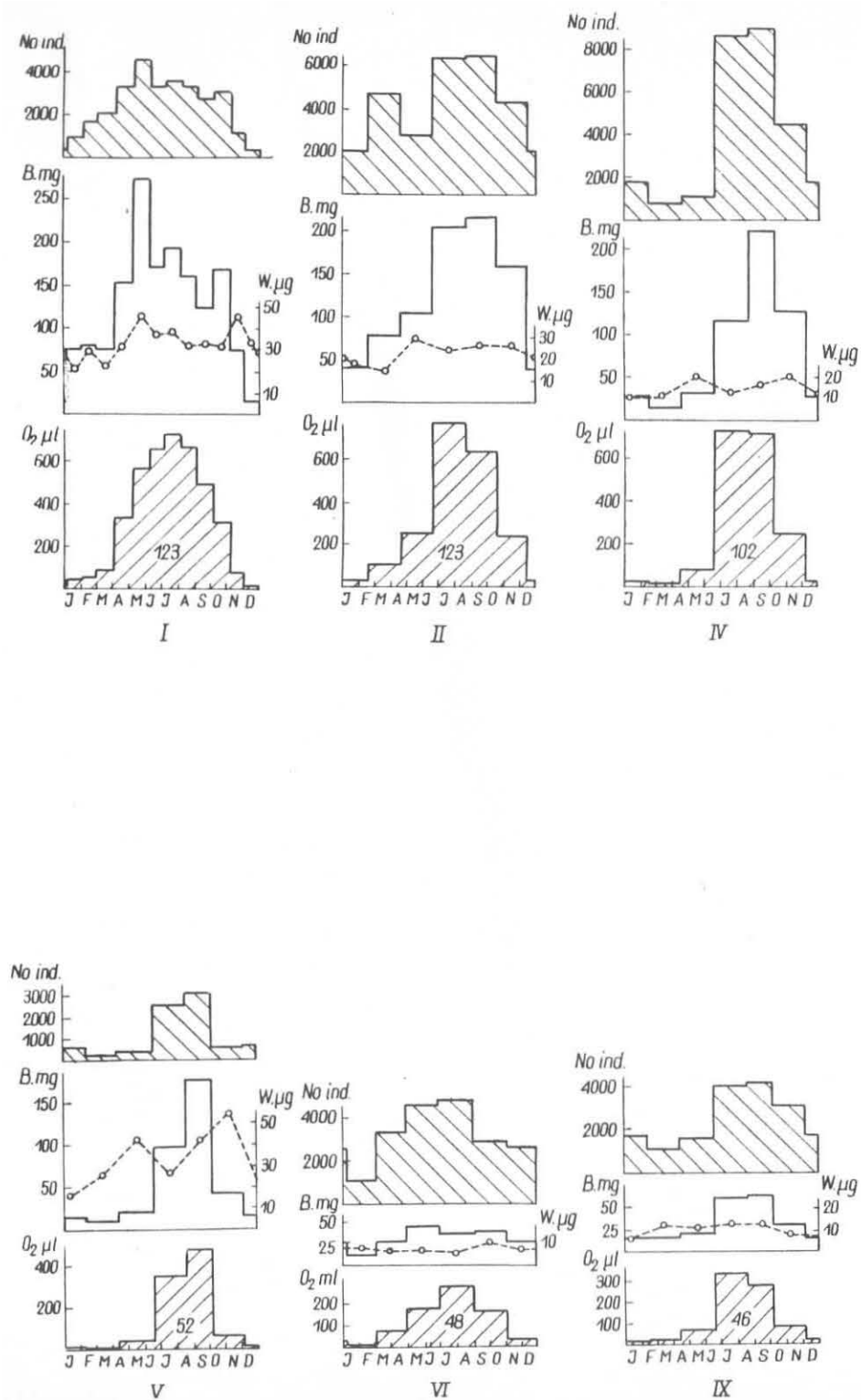| No of community	Mean number of ind. per 1 of litter	Mean biomass mg/l of litter	O₂-consumed ml/l/year
I	2,553	131	123
II	3,892	136	123
III	448	33	33
IV	4,278	90	102
V	1,233	60	52
VI	3,239	32	48
VII	4,441	53	64
VIII	1,666	36	44
IX	2,631	35	46
X	2,963	44	43
XI	1,451	33	33
XII	4,354	67	74
XIII	6,497	90	100

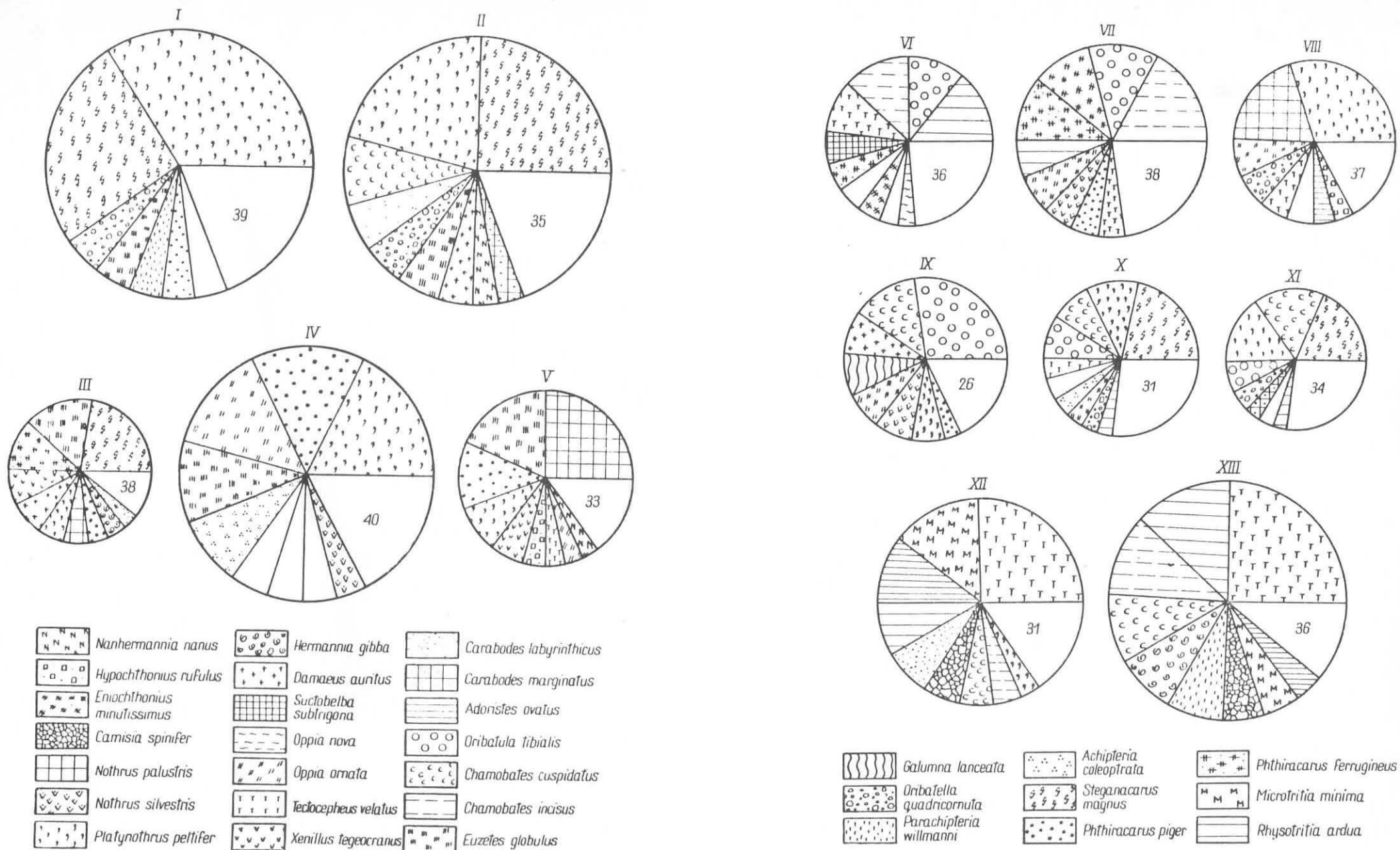Fig. 1. Fluctuation of density, biomass, average weight and oxygen-consumption in the different communities

Fig. 2. For explanations see text

Legend (left):
- Nanhermannia nanus
- Hypochthonius rufulus
- Eniochthonius minutissimus
- Camisia spinifer
- Nothrus palustris
- Nothrus silvestris
- Platynothrus peltifer
- Hermannia gibba
- Damaeus auritus
- Suctobelba subtrigona
- Oppia nova
- Oppia ornata
- Tectocepheus velatus
- Xenillus tegeocranus
- Carabodes labyrinthicus
- Carabodes marginatus
- Adoristes ovatus
- Oribatula tibialis
- Chamobates cuspidatus
- Chamobates incisus
- Euzetes globulus

Legend (right):
- Galumna lanceata
- Oribatella quadricornuta
- Parachipteria willmanni
- Achipteria coleoptrata
- Steganacarus magnus
- Phthiracarus piger
- Phthiracarus ferrugineus
- Microtritia minima
- Rhysotritia ardua